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The Importance of Phytoplankton Biomass as an Ecosystem Parameter in Shallow Bays of the Baltic. I. Relationships between Biomass and System Characteristics

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With 9 Figures

Key words: Hierarchical ecosystem structure, phytoplankton biomass, influencing factors, ecological requirements, shallow lagoons

Abstract

The importance of phytoplankton as a characteristic ecosystem component is closely connected with its position in the hierarchical ecosystem structure. Because of the relations to the levels below and above, phytoplankton biomass and composition integrate characteristic properties of the ecosystem. The information content of these parameters has been demonstrated for data from a tenyear-monitoringseries in the western branch of the Oder-estuary. Over all, phytoplankton species composition in coastal waters is closely correlated with salinity and temperature, biomass concentration first of all with the trophic level. Cyanobacterial blooms are attributable to physical processes and are not necessarily indicators for eutrophication.

1. Introduction

In the hierarchical structure of a pelagic ecosystem, phytoplankton represents the level of primary producers. Its physiological and ecological efficiencies are controlled by "bottom-up" effects from the abiotic ecosystem basis and by "top-down" effects from the superordinated levels of consumers (LAMPERT & SOMMER 1993). Phytoplankton assemblage characteristics, such as species composition, biomass, chlorophyll *a* and primary production, result from the intricate cooperation of these effects. Therefore, phytoplankton parameters integrate essential properties of the ecosystem.

In shallow lagoons where long retention times favour growth of phytoplankton, biomass of these autotrophs is an ecological indicator of special importance and not replaceable by others; the relationships to different environmental factors are complex and intricate. Phytoplankton biomass and composition in such ecosystems result from the conditions governing primary production, from grazing and from the ecological requirements of the organisms themselves. Because of these causal relationships, the estimation of phytoplankton biomass in a monitoring programme is not the end in itself, but must be analysed in connection with the environmental factors involved.

The following text is the first part of a study demonstrating the importance of phytoplankton biomass as a key indicator in shallow coastal waters by monitoring results from the western branch of the Oder-estuary. In this system, particularly in the eutrophic "Kleines Haff" (Kl.H.), primary production is almost entirely due to phytoplankton. In the mesotrophic "Greifswalder Bodden" (Gr.B.) also macrophytes are present, but phytoplankton organisms are the major autotrophs. The study is focused on the *importance* of phytoplankton biomass as *ecosystem parameter*. With regard to the problems concerning the characterization of coastal waters by representative ecosystem properties, the subject is of scientific interest as well as of practical importance for the public authorities responsible for monitoring and water management.

2. Material and Methods

The monitoring programme was conducted from 1972–1981 by the former Water Management Board in Stralsund, currently "Staatliches Amt für Umwelt und Natur", the appropriate authority for monitoring and management of the adjoining coastal waters. Chemical analyses were completed in the chemical laboratories of the former "Hauptlabor" (direction: G. SCHOKNECHT), biological investigations by the author. Physical and chemical data were determined

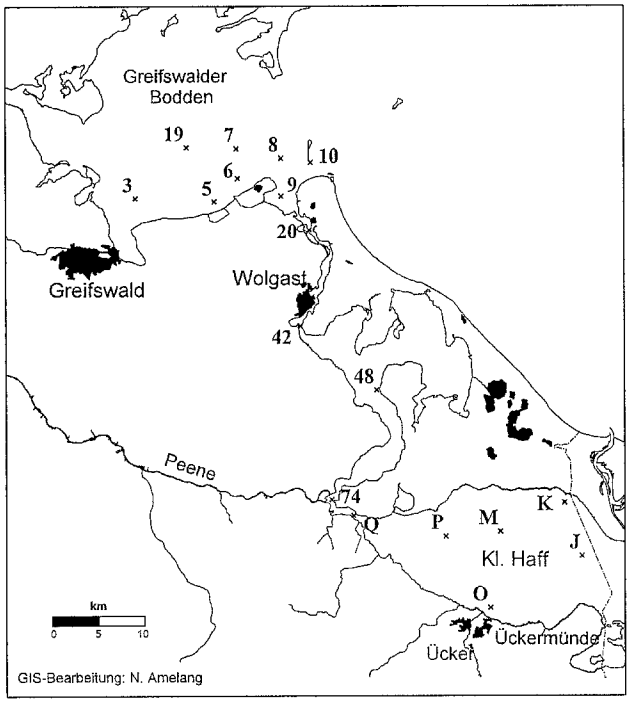

Fig. 1. The western branch of the Oder-estuary with the monitoring stations.

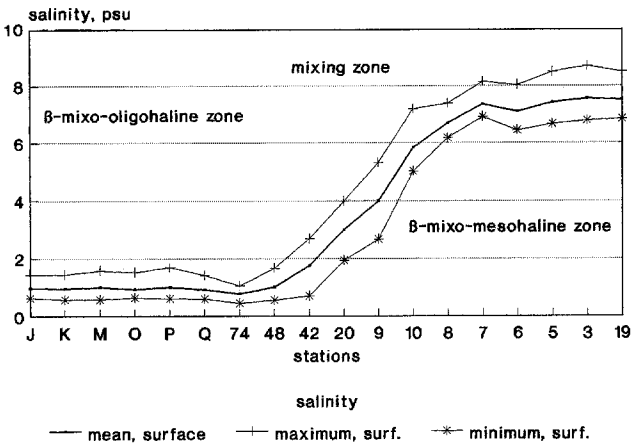

Fig. 2. Salinity. Average, maximum and minimum of annual means 1972–1981.

with standard methods according BREITIG & VON TÜMPLING (1975), biomass using the UTERMÖHL-technique (EDLER 1979), and taxonomical composition according to CLEVE-EULER (1968), PANKOW (1976) and PASCHER (1925 ff.). A more detailed description of the programme and the methods used and more figures are presented in SCHMIDT (1990a) and an unpublished GOAP-report (SCHMIDT 1994b). To demonstrate the importance of phytoplankton properties as ecosystem parameter, the relationships of phytoplankton biomass and composition to different environmental factors and their co-operation during the year are analysed.

Hydrography, morphometry and water resources of the western part of the Oder-estuary have been frequently investigated (LAMPE 1996). The German part of the estuary is characterized as a chain of unstratified lagoons with inverse gradients of salinity and the degree of eutrophication. The Oder-river is the main source of water and dissolved matter. Other rivers, Ücker (Kleines Haff), Peene (Peenestrom) and Ryck (Greifswalder Bodden), are minor contributors. Waterexchange with the adjacent Baltic Sea mainly depends on weather conditions and river run-off (Fig. 1).

3. Results

3.1. Phytoplankton and influencing factors

The main bottom-up factors influencing phytoplankton composition and biomass are salinity, water temperature, light conditions and nutrients; the most important top-down factor is zooplankton grazing. Salinity increases toward the estuary (Fig. 2) and causes a distinct spatial diversity of phytoplankton composition in the system. Salinity conditions and the special salinity requirements of the phytoplankton species involve the division of the estuary in different ecological zones with more or less strictly adapted populations. Using the "Venice-system" (CASPERS 1959), the upper parts, Kleines Haff and Oberer Peenestrom with a mean salinity of 1 psu, belong to the β-mixo-oligohaline zone (β-oligohaline z.); the lower part, Greifswalder Bodden with a mean salinity of approximately 7 psu, is a β-mixo-mesohaline zone (β-mesohaline z.). Both zones are connected by a region of intensive water exchange and mixing at Unterer Peenestrom and Peenestrommündung.

According to the classifications in "Ostsee-Algenflora" (PANKOW 1990) oligo- to meso-euryhaline freshwater species are dominant in the β-oligohaline zone (Kl.H.). Meso- and pleio-euryhaline freshwater species and marine organisms of different halobity and salinity tolerance inhabit the β-mesohaline zone (Gr.B.). The total number of taxa in both zones approximate the same order of magnitude (Fig. 3). In the mixing-zone no species minimum, expected due to salinity induced mortality, was detectable. In contrast, due to water exchange and mixing, the total number of phytoplankton taxa was distinctly higher than in the adjacent salinity-zones. This fact indicates that a stable β-mixo-oligohaline zone with an adapted phytoplankton population is missing in this sphere. Total biomass in both ecological zones was not directly affected by salinity. However, because of the inverse gradients of salinity and trophic level in the estuary, changes of main biomass are linked with inverse changes in salinity (Figs. 2 and 8).

Temperature conditions are affecting the species composition as well as the rates of physiological processes. Therefore, phytoplankton biomass and composition change during the year. In spring and autumn, cold-water species, mainly

diatoms, dominated in both salinity zones, while in summer Cyanobacteria and Chlorophyceae, adapted to higher water temperature, were most common. In spring, the typical diatoms of the β-mesohaline zone (Gr.B.), *Achnanthes taeniata*, *Sceletonema costatum* and *Chaetoceros* spp., are strongly limited to a narrow range of low temperature (SCHMIDT 1990a).They are stenotherm in contrast to the more eurytherm cold-water forms of the β-oligohaline zone (Kl.H.), e.g. *Sceletonema subsalsum* (Figs. 5 and 6). Notably, this is in context with the slower warming up in the β-mesohaline zone (Fig. 4). Low temperature optima enable the spring diatoms to reproduce at 0–4 °C. With rapidly increasing temperatures in April/May they form resting stages and eventually disappear from the water column. According to the stenotherm character of the dominants, in the Gr.B. a sharp reduction in total biomass (Fig. 7a) happens after March/April. In the β-oligohaline zone (Kl.H.) spring diatoms also decrease in April/May coincidently with the rising temperature, but more slowly, and not always completely disappear (Fig. 6). Therefore, in this zone spring and summer phase are not separated so distinctly as in the β-mesohaline zone (Fig. 7b). In summer, biomass of the warm-water forms increased with increasing water temperature in both salinity zones; short-term biomass declines in summer were attributable to extraordinary high water temperatures of about 24 °C as well as to short-term cool-water events. In autumn, the decline in biomass was again coincident with the decline in temperature.

Also interannual differences in phytoplankton corresponded to the variability of temperature conditions, espe-

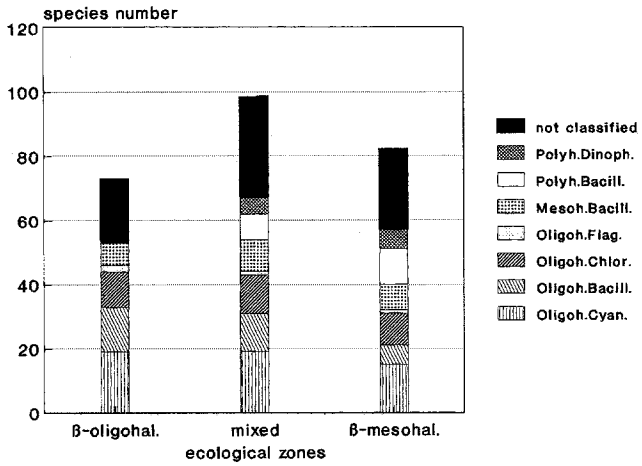

Fig. 3. Phytoplankton. Species numbers recorded in the salinity zones.

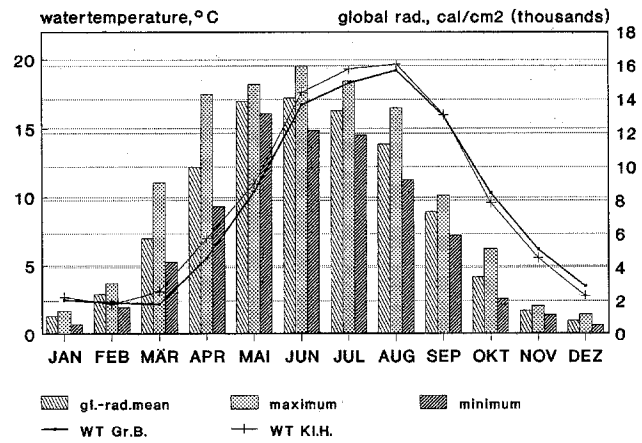

Fig. 4. Water temperature Kleines Haff (Kl.H.) and Greifswalder Bodden (Gr.B.), monthly means 1972–81; global radiation, monthly means 1972–1981, maximum and minimum (Maritimes Observatorium Zingst, measuring station Greifswald).

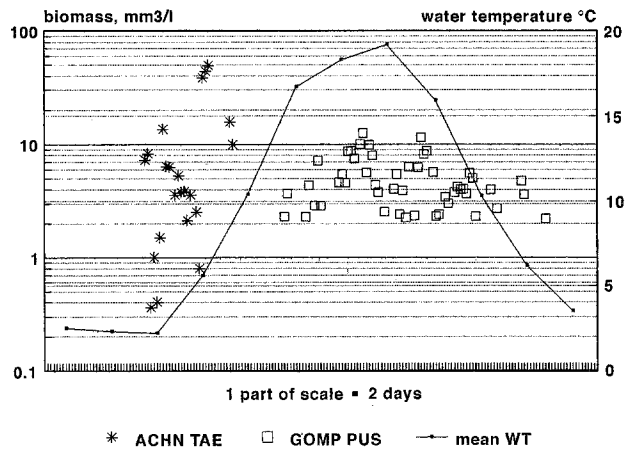

Fig. 5. Water temperature and biomass, *Achnanthes taeniata* and *Gomphosphaeria pusilla*, Greifswalder Bodden.

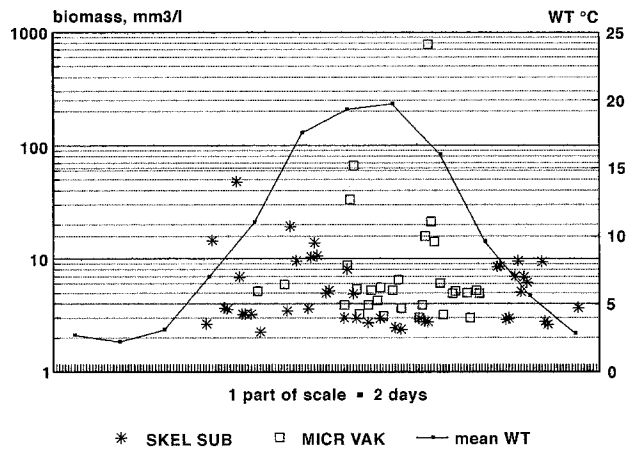

Fig. 6. Water temperature and biomass, *Sceletonema subsalsum* and *Microcystis*-species with gas vesicles, Kleines Haff.

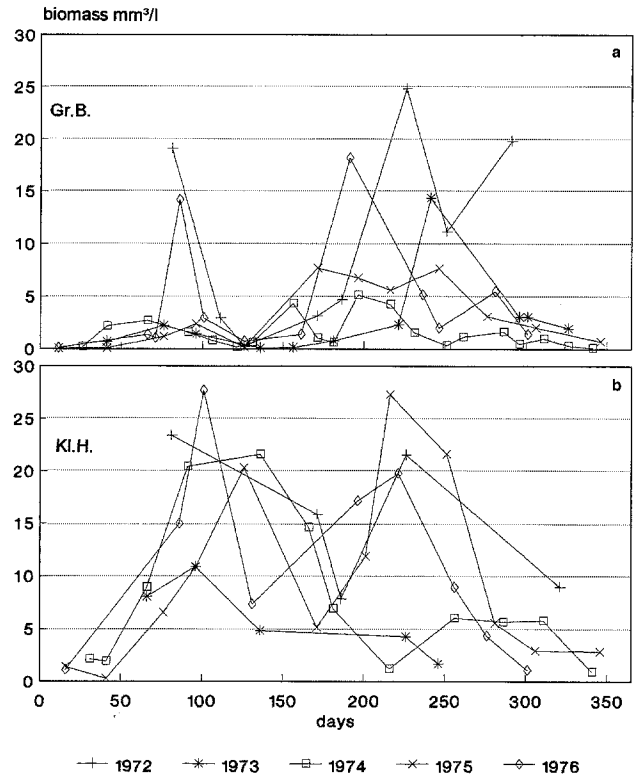

Fig. 7. Phytoplankton biomass 1972-1975. **a**: Greifswalder Bodden (Gr.B.); **b**: Kleines Haff (Kl.H.).

cially in spring. According to SCHMIDT (1990a), in the mesohaline Gr.B. other species of diatoms were dominant and phytoplankton growth was leading to distinctly higher biomass after a cold winter with a long ice-period than after a mild winter without ice formation. According to BRENNING & KELL (1990), HINRICHS (unpubl.), such temperature induced differences give rise to secondary differences in the phytoplankton urged "bottom-up" control of higher levels of the food-chain.

Relationships between phytoplankton and global radiation are similar to those for temperature, and it is difficult to distinguish the effects of both factors. An interesting phenomenon observed in phytoplankton taxa adapted to low temperature is the occurence of species with one growth period in spring and others with two periods of growth in spring and autumn. This may be due to different responses and requirements for radiation intensity, because low temperatures in spring are connected with higher radiation intensities than in autumn (Fig. 4). Total phytoplankton biomass follows the course of global radiation only in spring and autumn. Trend differences in summer and small biomass at highest radiation intensity indicate that from May to August other factors are controlling phytoplankton biomass. Direct disturbances of bioproduction by high radiation intensities may also occur.

The main input of the nutrients N, P and Si is attributable to Oder-river flow. Corresponding to the gradient in the annual mean of phytoplankton biomass, mean nutrient concentrations are decreasing in the same direction (Fig. 8). Temporary and regional disturbances in continuity are caused by inputs from Uecker (St.O) and Peene (St.74) rivers and by municiple load (St.20, 9). N-, P- and Si-concentrations in early spring, with the N:P-ratio far exceeding that of the Redfield

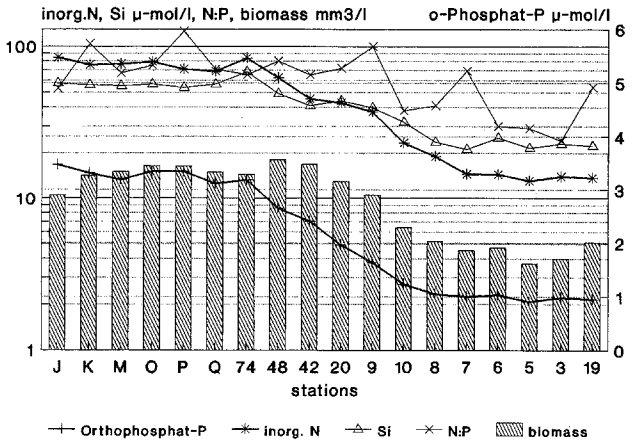

Fig. 8. Gradient of nutrients and biomass in the estuary, mean concentrations.

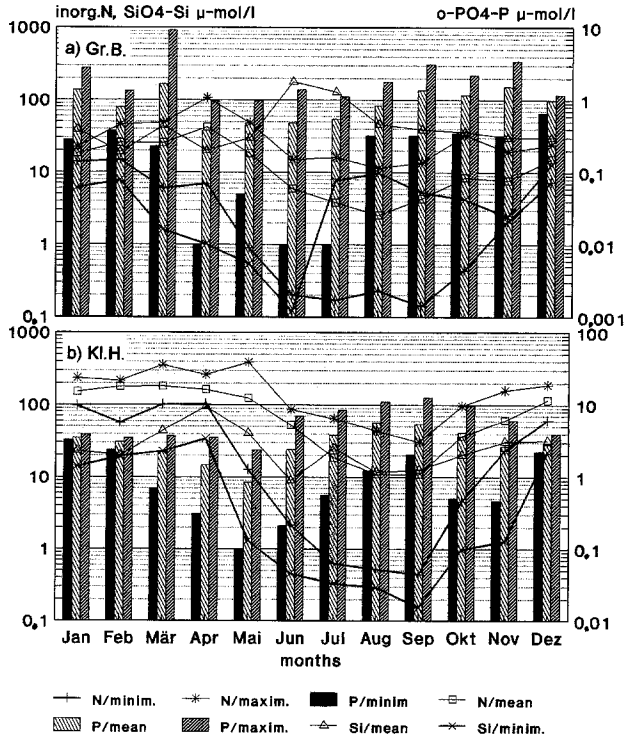

Fig. 9. Nutrient conditions. **a**: Greifswalder Bodden (Gr.B.); **b**: Kleines Haff (Kl.H.).

ratio (16:1), are a function of river input. In March/April, inverse changes of nutrient concentrations and biomass and the decrease of the N:P-ratio reflect the consumption by the autotrophs. Biomass minimum in May (April to June) corresponds to minima or low concentrations of Si, P and/or N (Fig. 9a and b), especially in the mesotrophic Gr.B. Therefore, the origin of the "breakdown" of the spring populations and of the more or less distinct phytoplankton lacking interphase between spring and summer phase in this zone, formerly was interpreted as a symptom for the dominant role of nutrients (Si, P or N) in phytoplankton production control (SCHNESE 1973). However, this thesis must be rediscussed with regard to the influences of temperature and zooplankton noted in 1972–1981. In summer, small or lacking nutrients in the water column do not exclude further biomass production (SCHMIDT 1990b). Consumption of inorganic N sources can proceed in Gr.B. up to an extreme N-deficiency (Fig. 9a), leading to the growth of N_2-fixing Cyanobacteria (SCHMIDT 1994a). Because of these relationships nutrient levels in shallow coastal waters and their importance for phytoplankton control cannot be evaluated by measuring exclusively the nutrients.

Phytoplankton distribution in the estuary sometimes is governed also by physical processes. Especially, the accumulation of Cyanobacteria with gas vesicles at the water surface under calm atmospheric conditions and horizontal drift of the colonies by low winds induce a horizontal and vertical patchiness, disturbing the perceptibility of causal relationships between biomass production and influencing factors. Such "waterblooms" occur in both salinity zones, but with different extent and a different manner of origin. In the eutrophic β-oligohaline zone (Kl.H.), mass development of *Microcystis*-species is typical for the summer phase. By rising to the surface during sunny and calm weather conditions, these procaryotes may form vast carpets at the surface with biomass reaching 800 mm^3/l (September 1979 in the eastern Kl.H.). In the mesotrophic β-mesohaline zone (Gr.B.) no phytoplankton mass development was noted in summer and the dominating species, *Gomphosphaeria pusilla*, does not possess gas vesicles. But with increasing N-deficiency, N_2-fixing Nostocaceae with pseudovacuoles, *Anabaena lemmermannii* or *Nodularia spumigena*, appear. Distributed in the whole water column, their biomass did not exceed 2 mm^3/l; but under favourable weather conditions, within few hours, the concentration processes described may lead to a biomass accumulation, approximating in small circumscribed areas the high concentrations registrated in large areas of the eutrophic upper parts of the estuary (SCHMIDT 1991, 1993/94, 1994a). In the first case eutrophication, mass development and physical processes gave rise to the water bloom, in the second case the same physical processes, but N-deficiency and no mass development were the causes.

Zooplankton were not estimated in the monitoring programme. According to BRENNING (1989), the strong decline in phytoplankton biomass after spring is partially attributable to zooplankton grazing. Furthermore, phytoplankton species composition influences species composition of zooplankton grazers. For example, the specific phytoplankton populations arising from given temperatures in spring in the β-mesohaline zone are followed by specific zooplankton populations (BRENNING & KELL 1990; HINRICHS, in prep.). Because of these relationships the information content of phytoplankton parameters is reduced, if zooplankton estimations are missing.

3.2. The co-operation of influencing factors in the annual course

Species and biomasses found in the estuary during the monitoring period always resulted from interactions between several controlling factors. Therefore, they are balance data and only precautiously explainable by the other monitoring data, mediating not all informations needed for a conclusive interpretation. For this, more complete knowledge about nutrient metabolism (total P and N, nutrient in- and output) and phytoplankton (distribution in the water column, interactions with competitors and consuments) is required. Nevertheless, a hypothetic conception on the co-operation of the environmental factors controlling phytoplankton biomass may be derived from the monitoring results.

As demonstrated by the relationships between phytoplankton composition and environmental factors, bioproduction in the estuary is due to phytoplankton organisms well adapted to these factors. Salinity operates over the entire year as a key regulator and explains different assemblages between the salinity zones. The seasonal changes in phytoplankton composition are explainable first of all by different responses and requirements to temperature. Probably, adaptations to global radiation also occur. In summer N-deficiency gives rise to an ecological niche for N_2-fixing Cyanobacteria.

Biomass production by the adapted phytoplankton assemblages in both salinity zones starts in january to april, dependent on the length of the ice-period and the transparency of ice. Because of the rapid increase of radiation in this period, the development of the spring diatoms is fundamentally affected by the date of starting. As in early spring nutrients are available in the whole estuary and zooplankton grazing may be negligible, water temperature and light are the main controlling factors in the first phase of phytoplankton growth. These conditions change with increasing biomass and proceeding season. Due to increasing consumption (and decreasing river input), the nutrients diminish, mostly attended by the decline of the N:P-ratio; coincidentally zooplankton grazing gets increasing importance. The disappearance of the spring forms corresponds in the whole water chain to rising temperature, rising global radiation, more or less distinct nutrient deficiency, a low N:P-ratio and high zooplankton activity. According to SCHNESE (1973) nutrient deficiency (Si, P or N) is the essential to the "breakdown" of phyto-

plankton assemblages in spring. With regard to the stenothermal character of the spring diatoms, and according to the zooplankton activities demonstrated by BRENNING (1989), this interpretation is not at all sustainable. The discussion of the new aspects, derived from the monitoring results 1972-81, would exceed theme and available space and shall be the subject of the next part of this study.

In summer phytoplankton composition in the estuary is mainly due to salinity and temperature. With regard to the unfavourable nutrient conditions at the beginning of the summer phase, adaptations of the dominants to low nutrient concentrations may also occur. The question for the N-resources enabling the growth of *Gomphosphaeria pusilla* in the Gr.B. in periods with inorganic N not detectable in the water column, is still unreplied. In summer phytoplankton biomass in the estuary is more or less controlled by light, temperature, nutrients and zooplankton grazing. In the β-oligohaline zone (Kl.H.) no distinct symptoms of nutrient limitation were observed in the investigation period. The high biomasses correspond to the high trophic level. The decrease of the N:P-quotient, caused by different use and delivery of N and P, was never leading to the development of N_2-fixing Cyanobacteria. Therefore, climatic conditions and zooplankton are regarded as the more important factors. In contrast, in the β-mesohaline zone (Gr.B.), N-deficiency produced in some years an ecological niche for N_2-fixing Cyanobacteria. Therefore, in this zone availability of N is most important for bioproduction progress in summer. The waterblooms happening in summer in the whole estuary disturb the perceptibility of causal relations between biomass and influencing factors. Hence, the evaluation of eutrophication processes from air photos of such situations needs also direct investigations on nutrients and organisms involved.

In autumn/winter a second change of phytoplankton composition takes place, induced by the decline of temperature, perhaps also of radiation intensity. In the β-oligohaline zone the same species appear as in spring, but in the β-mesohaline zone, most of the cold stenotherm forms are missing. Because of the temperature adaptation of the dominating species and the availability of nutrients, the decrease of biomass in this period is regarded as an effect of light deficiency.

4. Conclusions

As shown for a tenyear monitoringseries from the western part of the Oder-estuary, phytoplankton composition and biomass as well as their spatial and temporal variability are informative parameters to characterize the properties of this shallow coastal waters, to understand trophic processes and to assess transport processes in the estuarine system. Beneath total phytoplankton biomass, biomasses of the dominant species are of special importance for the interpretation of causal relationships between phytoplankton and the most important controlling factors. Their comparison with attendant autecological data leads to informations about the ecological responses and requirements of the operating taxa themselves, that are not derivable from anonymous parameters as total biomass or chlorophyll *a*. Taking the special reply of the dominant phytoplankton species in consideration, the, hitherto, more one-sided interpretation of biomasses as an effect of interacting environmental factors, can be improved. As pointed out above, new ideas on the interactions of the biomass controlling factors and their importance in the estuary (to be presented in detail in part 2 of the study) are derived in this way from the monitoring results. Furthermore, the yield of informations achievable from biomass data, favours the UTERMÖHL-technique for monitoring aims and justifies the great expense of time for it.

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